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# Network analysis reveals humans as top predators and the key role of cuttlefish in the food web structure of a marine protected area (Arrábida Natural Park)

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ABSTRACT

The marine protected area (MPA) of the Arrábida Natural Park is a mid-latitude hotspot for biodiversity. To understand its trophic structure, a highly defined food web network was assembled for this ecosystem, consisting of 884 taxa. Network analysis showed that humans are the top predators, as well as various seabirds, dolphins and sharks. This web is dominated by intermediate species, and its general organization follows previously reported patterns for other marine and coastal ecosystems. Two swimming crabs, *Polybius navigator* and *Polybius henslowii*, assume important roles as mid-trophic level consumers and prey, due to their high connectivity in the network. The cuttlefish, *Sepia officinalis*, a cephalopod of high commercial value, assumes the most pivotal role in the network, as it is the species with the highest number of prey and is among the top 10 most highly connected species (with more links to other species). Additionally, the cuttlefish is among the species with shortest path length, that is the lowest number of links connecting it to any other species. Since, this cephalopod is highly mobile and extends its territory outside the MPA, into the Sado estuary, where it is the main target of local fisheries, and is exposed to various pollution sources, close monitoring the local population of cuttlefish is of the utmost importance, not only in the Arrábida MPA but also in the adjacent Sado estuary.

## 1. Introduction

The Marine Park of the Arrábida Natural Park is a biodiversity hotspot that stretches over a 38 km coastline in the West coast of Portugal. It lies at a biogeographical transition zone at mid-latitude between temperate and subtropical climates, where temperate, subtropical and even some tropical species coexist, leading to high levels of biodiversity (Briggs, 1974; Gonçalves et al., 2002; Henriques et al., 2007; Vinagre et al., 2011).

More than 1320 species of marine flora and fauna have been reported for this area, including a high number of macroalgae, benthic invertebrates, and fish species (Henriques et al. 2007; Horta e Costa et al., 2014). Filter feeding bivalves are particularly abundant (Gonçalves et al. 2002). There is seasonal growth of dense macroalgal beds of *Asparagosis armata, Cystoseira usneoides* and *Saccorhiza polyschides*, which form structurally complex habitats for numerous invertebrate and fish species (Gonçalves et al. 2002). Ichthyofaunal diversity includes both resident and transient species, with wrasses and sea breams being the most frequently observed fish (Gonçalves et al. 2002).

This area was designated a marine protected area (MPA) in 1998, as a way of responding to extensive habitat degradation (Carneiro, 2011). This was mostly caused by intensive fishing, but also by recreational nautical activities (Cunha et al., 2014; Pita et al., 2020). The anchoring of boats combined with bivalve dredging severely depleted the seagrass meadows of *Zostera marina*, which used to cover a large extension of the park area (Cunha et al., 2014). Hence, the marine park was established with the purpose of not only preserving what remained of the ecosystem but also to recover the overexploited habitats and species, to support scientific research and to develop a future scenario of sustainable practices, because this region includes towns where local people depend on fishing for subsistence (Batista et al., 2011; Cunha et al., 2014; Pita et al., 2020). The marine protected area comprises three protection

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levels, including a no-take area of ca. 4 km$^2$, where human presence is generally not allowed (Batista et al., 2011). Fishing is allowed in most of the park area but under restrictions (Batista et al., 2011).

In the middle of this MPA lies one of the largest fishing harbours in Portugal, Sesimbra. In 2023, Sesimbra reported the highest landings in Portugal, with a total of 30 431 t (Instituto Nacional de Estatística, 2024). The chub mackerel, *Scomber colias,* horse mackerel, *Trachurus trachurus*; the sardine, *Sardina pilchardus*; and the Black scabbardfish, *Aphanopus carbo*, were the most landed species (in weight) (Instituto Nacional de Estatística, 2024). Batista et al. (2015) reported that the top species in landings per unit of effort (kg day$^{-1}$ vessel$^{-1}$) of vessels licensed to fish within the MPA were the octopus, *Octopus vulgaris*, the cuttlefish, *Sepia officinalis*, and various sole species, *Solea* spp.

Pita et al. (2020) in a study comparing surveys from 2007 to 2015, reported that local fishers' acceptance of the MPA was low and contentious at the implementation phase (Vasconcelos et al., 2012; Horta e Costa et al., 2013; Stratoudakis et al., 2015) and did not improve over time. Poor enforcement and low compliance with regulations, results in illegal fishing taking place within this MPA (Cunha et al., 2011).

Nevertheless, the establishment of this MPA prompted a series of scientific surveys that resulted in an improved understanding of the ecology of this coastal ecosystem and in the development of a highly defined database of the species occurring in the area. These data allow the assemblage of the most highly defined food web at mid-latitudes to date. The aim of the present study is to describe the complex topology of the food web of the Arrábida Marine Park, compare its network properties to previously studied coastal food webs, and investigate species of particular importance in the trophic web.

The approach used is based on a binary predator-prey matrix and explores the topology of such relations in the resulting network, integrating complex network analysis and food web ecology, as proposed by May (1973) and Pimm (1982) and the many others who followed in the investigation of trophic networks topological patterns and response to disturbance (e.g. Williams and Martinez, 2000, 2004; Dunne et al., 2004; Bascompte, 2009; Coll et al. 2011; Vinagre and Gaston, 2024).

Food web network theory provides a robust framework for understanding the organizational structure of ecological communities by modeling trophic interactions as complex networks. In this approach, species are represented as nodes and their feeding relationships as directed links, allowing researchers to quantify and compare key network properties such as connectance (proportion of realized links over all possible links) and degree distribution (distribution of links per species) (e.g. Dunne et al., 2004; Bascompte, 2009; Coll et al. 2011; Vinagre and Gaston, 2024). This network-based perspective reveals emergent patterns that are not apparent from species-level analyses alone and offers insights into the structural organization and robustness of ecosystems (Dunne et al. 2002; 2004; Mendonça et al., 2022). Moreover, food web network theory facilitates the identification of keystone species and critical interaction pathways through the detection of highly connected species and top trophic level species, aiding in the development of targeted conservation strategies (Dunne et al., 2004; Cirtwill et al., 2018; Vinagre et al., 2019; Vinagre and Gaston, 2024).

The assemblage of a complex food web network for the Arrábida MPA is an important step in the investigation of this ecosystem since it not only provides the food web network analysis presented in this work but also the structural network for future coupling of biomass and energy fluxes, for a future ecological dynamics approach.

## 2. Materials and methods

### 2.1. Study area

The coastal area where the Arrábida Marine Park is located is characterized by south oriented high vertical cliffs that protected the area from the prevailing cold northern winds (Fig. 1). The gradual disintegration of the calcareous cliffs forms a heterogeneous subtidal environment, dominated by large rocks and boulder fields down to ca. 20 m depth (Gonçalves et al., 2002), bordered by sandy bottoms down to ca. 100 m depth, in the western limits of the park. The eastern section of the park is shallower with sandy bottoms down to 30 m deep. This area harboured extensive seagrass beds, which were progressively lost by the end of the 20th century (Cunha et al., 2009; A.H. 2011). They became completely extinct in 2007, but *Zostera marina* was reintroduced in 2011, and has persisted and increased until the present date (Paulo et al. 2019), and were recently increased in area with further seagrass restoration (Mourato et al. 2023).

Coastal upwelling is prevalent during summer (Lemos and Pires 2004). Mean sea surface temperature ranges between 14 °C-17 °C in

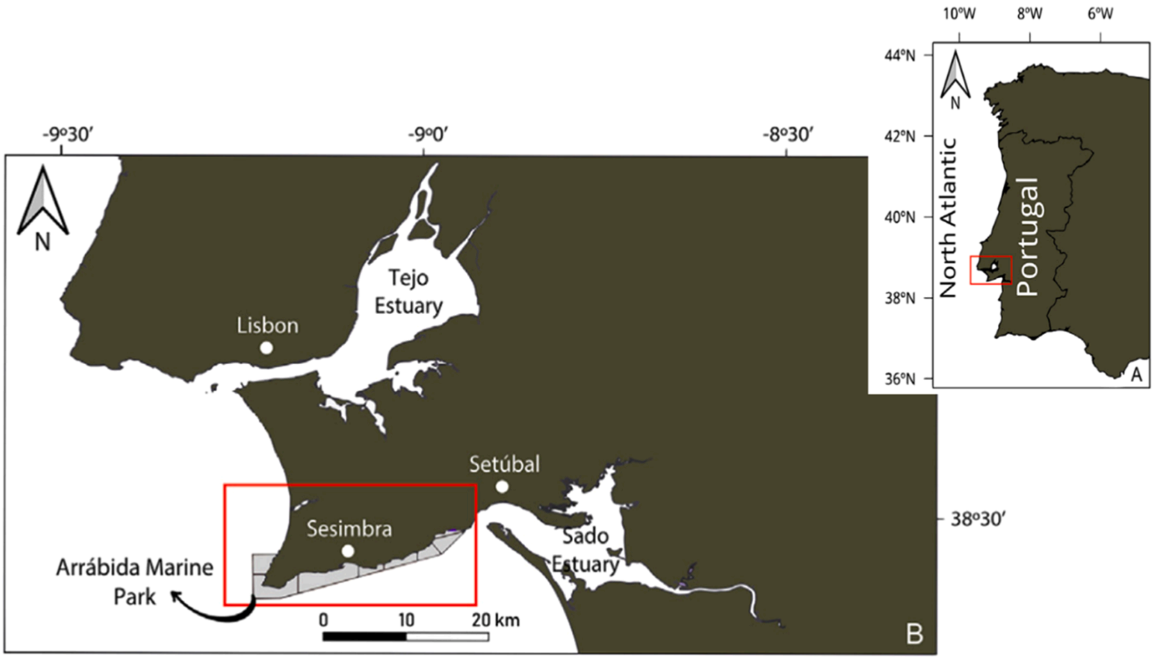

**Fig. 1.** Location of the study site in Portugal (A) and of the Arrábida Marine Park in the Setúbal Peninsula (B).

winter and 17 °C-22 °C in summer (www.seatemperature.org).

### 2.2. Food web assemblage

The database compiled in the INFOBIOMARES project (available in the geoportal of https://arrabidaparquemarinho.ualg.pt/, downloaded in 2022) was used in the present study. A list of species recorded for more than two centuries in the marine park (records range from 1797 to 2021) was assembled encompassing 1808 taxa. Extremely rare species, with ≤ 2 records were excluded from the analysis, as well as taxonomically redundant entries. *Homo sapiens* was added to the species list, given that fisheries (both legal and illegal) occur inside the study area making humans effective predators of various species (Batista et al., 2011; 2015). General nodes of aggregated taxa were added to the list representing detritus, phytoplankton and Insecta. The final list contained 884 taxa, most of them defined to the species level (Supplementary material 1).

### 2.3. Food web network

A binary matrix depicting predator-prey relationships was produced (Supplementary material 2) based on published literature anywhere in the world (Supplementary material 3), assuming that if a species consumes the other in another ecosystem it will do so too in our study area. Parasites were also included to ensure that the diversity and complexity of the food web was thoroughly accessed (Dunne et al. 2013).

The food web networks established were based on trophic species (=trophospecies). Meaning that groups of taxa with the same predators and prey are aggregated into one trophic species (Briand and Cohen, 1984). This is a convention used in this kind of study, aimed at reducing methodological biases due to uneven resolution of taxa within and among food webs (Briand and Cohen, 1984; Williams and Martinez, 2000). The trophic network was produced using the software Network3D (freely available upon request to the corresponding author), as well as in all other calculations (Yoon et al., 2004; Williams, 2010).

A total of 18 network properties were calculated (Table 1), including one diversity metric: number of trophic species (S); two metrics of trophic interaction: links per species (L/S) and connectance (C); and six metrics that indicate the proportion of species trophic types: top species (T), basal species (B), intermediate species (I), cannibal species (Can), herbivores plus detritivores (H), and omnivore species (Omn). Resource and consumer count were calculated for each trophic species.

Network structure properties were also estimated (Table 1): mean shortest chain to a basal species (Chain); characteristic path length (Path); mean shortweighted trophic level (TL); clustering coefficient (Clust); standard deviation of mean generality (GenSD); standard deviation of mean of vulnerability (VulSD); and normalized standard deviation of number of links (LinkSD).

Network properties calculated for the present study were compared to previous studies that used the same equations to calculate structural network properties in complex food webs for other marine ecosystems and other ecosystems, such as coastal lagoons, intertidal reefs and seagrass meadows (Table 2).

Tables were produced with the top 10 species for trophic level, connectivity (total number of links), generality, vulnerability and shortest path length, to allow the identification of particularly relevant species in the network. Parasites were included in the food web network, to ensure the analysis of the full complexity of the network, however they were not selected for the top 10 analyses given that their relationship with other species is not one of predation.

The number of consumers was plotted with the number of resources, using the original species list (before aggregation of species into trophic species), to identify the distribution of supergeneralist species (defined here as predators with ≥ 90 prey species) (Fig. 2)

**Table 1**
Definition of the network properties estimated.

| Food-web properties | | Description |
|---|---|---|
| Number of trophic species | S | Number of nodes in the network = Number of species in the food web after conversion to a trophic web |
| Links per species | L/S | Number of links per species |
| Connectance | C | Proportion of actual trophic links to all possible links |
| Top species | T | Fraction of species that have no predators or parasites |
| Intermediate species | I | Fraction of species that have both predators and prey |
| Basal species | B | Fraction of species that do not consume anything |
| Herbivores plus detritivores | H | Fraction of species that only consume basal species |
| Cannibals | Can | Fraction of species which prey on their own species |
| Omnivores | Omn | Fraction of species that are omnivores (consume prey at different trophic levels) |
| Resource count | - | Count of all species that serve as resources in the web |
| Consumer count | - | Count of all species that serve as consumers in the web |
| Short-weighted Trophic level | TL | Average of consumers' shortest trophic level (1+shortest chain to a basal taxon) |
| Mean shortweighted Chain length | Chain | Mean shortest chain to a basal species |
| Mean shortest path length | Path | Mean shortest path length between node pairs |
| Generality standard deviation | GenSD | Standard deviation of the number of resources per taxon |
| Vulnerability standard deviation | VulSD | Standard deviation of the number of consumers per taxon |
| Normalized standard deviation of links | LinkSD | Standard deviation of the number of number of links per taxon |
| Clustering coefficient | Clust | The mean shortest set of links between species pairs |

## 3. Results

The trophic network assembled presents 449 trophic species (supplementary material 4). Food web network properties were, in general, within previously reported ranges for other marine ecosystems and other coastal ecosystems (Table 2), except for the percentage of basal species, which was only 1 %, thus lower than reported for any ecosystem previously studied using similar methods (Table 2). Links per species, with a value of 57.3, was higher than previously reported for any marine ecosystem (Table 2). However, similar high values were previously reported for coastal lagoons, in Portugal (Table 2).

The species with the highest TL, 3.97, was *Homo sapiens* (Table 3). Other species in the top 10 TL were various large sea birds, three dolphin species - the harbour porpoise, *Phocoena phocoena*, the common dolphin, *Delphinus delphis*, and the bottlenose dolphin, *Tursiops truncatus* - and the sandbar shark, *Carcharhinus plumbeus*, with TLs ranging from 3.90 to 3.49 (Table 3). These top TL species included also the nudibranch *Piseinotecus sphaeriferus*.

The network node with the highest connectivity was Detritus, followed by various isopod, amphipod and polychaete species (Table 4). Two swimming crabs, *Polybius navigator* and *Polybius henslowii*, were also in the top 10 in connectivity, as were the cuttlefish, *S. officinalis*, and the finfish, *Gobius cobitis* (Table 4).

The species with the highest generality (highest number of prey) was the cephalopod, *S. officinalis*, followed exclusively by fish species, both bony fish and cartilaginous fish (Table 5). Among the bony fish were the bullet tuna, *Auxis rochei*, the dusky grouper, *Epinephelus marginatus*, the stargazer *Uranoscopus scaber*, the white seabream *Diplodus sargus*, the giant goby *Gobius cobitis*, and the scorpionfish *Scorpaena porcus* (Table 5). Among the cartilaginous fish were the houndshark, *Mustelus mustelus*, the eagle ray, *Myliobatis aquila*, and the thornback ray *Raja*

**Table 2**
Ranges of commonly reported values for food web properties for food web networks of different ecosystems. $N$= number of food web networks studied, $S$ = number of trophic species, $C$ = Connectance, L/$S$ = links per species, $T$ = % top species, $I$ = % intermediate species, $B$ = % basal species, Can = % cannibal species, Omn = % omnivorous species, TL = mean short-weighted trophic level (as defined in Williams and Martinez 2004), Path = mean shortest path length between node pairs. Ranges that do not totally overlap with those of marine ecosystem are presented in bold; ranges that do not totally overlap with any of those of other marine and/or non-marine ecosystems are underlined.

| Ecosystem | N | S | C | L/S | T | I | B | Can | Omn | TL | Path | Source |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Arrábida MPA | 1 | 449 | 0.13 | **57.3** | 12 | 86 | **1** | 13 | 85 | 2.8 | 1.8 | Present study |
| Sanak Islands near shore | 1 | 511 | 0.03 | 13.3 | 7.6 | 82 | 11 | 18 | 74 | 2.8 | 2.4 | Dunne et al. (2016) |
| Weddell Sea | 1 | 488 | 0.07 | 33.2 | 6.7 | 80 | 14 | – | 67 | 2.5 | – | Jacob et al. (2011) |
| Gulf of Alaska | 1 | 406 | – | 2.6 | – | – | – | – | – | – | 2.6 | Gaichas and Francis (2008) |
| Other Marine ecosystems ($S$ < 400) | 6 | 29–245 | 0.04–0.24 | 3.4–17.8 | 0–19 | 47–98 | 2–34 | 4–42 | 45–87 | 2.1–3.2 | 1.6–1.9 | (Opitz, 1996; Yodzis, 1998; Link, 2002; Dunne et al., 2004; Marina et al., 2018) |
| Seagrass meadows | 16 | 53–68 | 0.17–0.23 | 11.4–12.9 | 13–18 | 58–65 | 21–26 | 13–19 | 70–75 | 1.8–2.0 | 2.0–2.3 | Coll et al. (2011) |
| Intertidal tropical rocky reef | 1 | 72 | 0.14 | 10.1 | 18 | 76 | 6 | 35 | 85 | 2.6 | 1.8 | Vinagre and Mendonça (2023) |
| Intertidal Sub-Arctic (rock + sand) | 1 | 232 | 0.03 | 7.8 | 7 | 76 | 17 | 20 | 64 | 2.4 | 2.4 | Dunne et al. (2016) |
| Rock tide pools (cold, temperate and tropical) | 116 | 7–52 | 0.11–0.39 | 1.6–7.0 | 0–46 | 14–88 | 7–43 | 14–60 | 43–84 | 1.7–2.5 | 1.3–2.0 | Mendonça et al. (2018) |
| Coastal lagoons | 3 | 186–306 | 0.18–0.22 | 33.4–82.6 | 3–27 | 66–92 | 5–7 | 22–29 | 81–85 | 2.9–3.0 | 1.7 | Vinagre and Gaston (2024) |

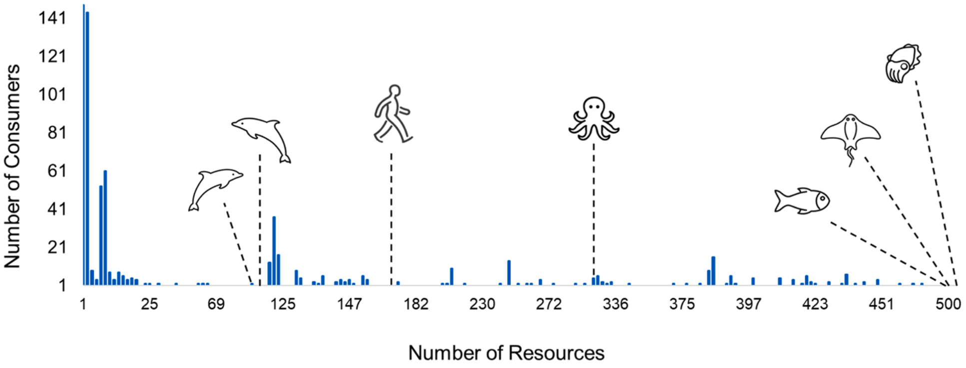

**Fig. 2.** Number of Resources per Consumer in the original species version of the food web of the Arrábida Marine Park, showing the top 3 species with highest number of prey species: the cuttlefish *Sepia officinallis* with 560 resource species, the eagle ray *Myliobatis aquila* with 507 resource species, and the fish *Diplodus sargus* with 500 resource species), highlighting the top TL predators with ≥ 90 prey species: *homo sapiens* with 168 resources species, the bottlenose dolphin *Tursiops truncatus* with 108 resource species, and the common dolphin *Delphinus delphis* with 90 resource species. Additionally, the position of the top species in landings per unit of effort in these fisheries, *Octopus vulgaris*, with 325 prey species, is also highlighted.

**Table 3**
List of trophic species in the top 10 trophic level.

| Rank | Trophic species | Trophic level |
|---|---|---|
| 1 | *Homo sapiens* (Humans) | 3.97 |
| 2 | *Piseinotecus sphaeriferus* (nudibranch) | 3.90 |
| 3 | *Leucothoe incisa* (carnivorous amphipod) | 3.74 |
| 4 | *Buteo buteo* (raptor) | 3.66 |
| 5 | *Stercorarius skua* (large seabird) | 3.58 |
| 6 | *Phocoena phocoena* (dolphin) | 3.52 |
| 7 | *Carcharhinus plumbeus* (shark) | 3.51 |
| 8 | *Delphinus delphis* (dolphin) | 3.51 |
| 9 | *Tursiops truncatus* (dolphin) | 3.50 |
| 10 | *Sula leucogaster* (large seabird) | 3.49 |

**Table 4**
List of trophic species in the top 10 of connectivity.

| Rank | Common Name | Connectivity |
|---|---|---|
| 1 | Detritus | 3.82 |
| 2 | *Eurydice pulchra* (isopod) | 3.26 |
| 3 | *Pseudoprotella phasma* (amphipod) | 2.46 |
| 4 | *Polybius navigator* (crab) | 2.45 |
| 5 | *Sepia officinalis* (Cephalopod, Cuttlefish) | 2.34 |
| 6 | *Phtisica marina* (amphipod) | 2.25 |
| 7 | *Polybius henslowii* (crab) | 2.24 |
| 8 | *Gobius cobitis* (finfish) | 2.23 |
| 9 | *Alentia gelatinosa* + *Subadyte pelúcida* (polychaetes) | 2.18 |
| 10 | *Apherusa jurinei* (amphipod) | 2.18 |

*clavata* (Table 5).

The network node with the highest vulnerability (highest number of consumers) was Detritus, followed by various species of isopods, tanaidaceans, and amphipods (Table 6). Detritus was also the node with the shortest Path (shortest number of links to any other node), followed by various species of amphipods, crabs, shrimps and isopods (Table 7). The cephalopod, *S. officinalis*, was ranked fourth in shortest Path length, while the swimming crabs, *Polybius navigator* and *Polybius henslowii*, were ranked third and sixth, respectively (Table 7).

The number of prey per consumer ranged from 1 to 560 (Fig. 2). The cuttlefish, *S. officinalis*, was the species with more resource species, with 560 prey, followed by the eagle ray *Myliobatis aquila*, with 507 prey, and *Diplodus sargus*, with 500 prey (Fig. 2). The octopus, *O. vulgaris*, one of the main targets of the local fisheries, presented 325 prey species, while humans, the top TL species in the network, have 168 prey species, and the dolphins *D. delphis* and *T. truncatus*, have 90 and 108 prey species, respectively (Fig. 2).

**Table 5**
List of trophic species in the top 10 of generality (number of prey).

| Rank | Trophic species | Generality |
|---|---|---|
| 1 | *Sepia officinalis* (cephalopod, Cuttlefish) | 4.10 |
| 2 | *Auxis rochei* (finfish, tuna) | 3.54 |
| 3 | *Epinephelus marginatus* (finfish, grouper) | 3.49 |
| 4 | *Mustelus mustelus* (shark) | 3.44 |
| 5 | *Myliobatis aquila* (ray) | 3.31 |
| 6 | *Uranoscopus scaber* (finfish) | 3.31 |
| 7 | *Diplodus sargus* (finfish) | 3.21 |
| 8 | *Raja clavata* (ray) | 3.00 |
| 9 | *Gobius cobitis* (finfish) | 2.98 |
| 10 | *Scorpaena porcus* (finfish) | 2.98 |

**Table 6**
List of trophic species in the top 10 of vulnerability (number of predators).

| Rank | Trophic species | Vulnerability |
|---|---|---|
| 1 | Detritus | 7.64 |
| 2 | *Anilocra physodes* (isopod) | 3.94 |
| 3 | *Tanais dulongii* (tanaidacean) | 3.91 |
| 4 | *Sphaeroma* sp. (isopod) + *Apseudes spinosus* + *Apseudes talpa* + *Apseudopsis latreillii* (tanaidaceans) | 3.91 |
| 5 | *Eurydice pulchra* (isopod) | 3.89 |
| 6 | *Cirolana cranchii* + *Conilera cylindracea* (isopods) | 3.89 |
| 7 | *Pseudoprotella phasma* (amphipod) | 3.89 |
| 8 | *Phtisica marina* (amphipod) | 3.89 |
| 9 | *Apherusa jurinei* (amphipod) | 3.89 |
| 10 | *Ampithoe gammaroides* (amphipod) | 3.89 |

**Table 7**
List of trophic species in the top 10 of lowest mean shortest path length (between node pairs).

| Rank | Trophic species | Path |
|---|---|---|
| 1 | Detritus | 1.02 |
| 2 | *Pseudoprotella phasma* (amphipod) | 1.41 |
| 3 | *Polybius navigator* (crab) | 1.41 |
| 4 | *Sepia officinalis* (Cephalopod, Cuttlefish) | 1.42 |
| 5 | *Phtisica marina* (amphipod) | 1.43 |
| 6 | *Polybius henslowii* (crab) | 1.44 |
| 7 | *Eurydice pulchra* (isopod) | 1.45 |
| 8 | *Philocheras monacanthus* (shrimp) | 1.45 |
| 9 | *Apherusa jurinei* (amphipod) | 1.47 |
| 10 | *Ampithoe gammaroides* (amphipod) | 1.47 |

## 4. Discussion

This study presents, for the first time, the complex food web network of the Arrábida Marine Park, placing it among the most highly defined complex food webs published to date, and the most defined at mid-latitudes (Table 2). Encompassing 449 trophic species, it is among the three most diverse food web networks reported, only surpassed by the nearshore food web of the Sanak Islands, in Alaska, with 511 trophic species (Dunne et al., 2016), and the Antarctic Weddell Sea shelf food web, with 488 trophic species (Jacob et al., 2011).

Food web network properties of this web generally fall within previously reported values for marine ecosystems and other coastal ecosystems, like coastal lagoons, estuaries and intertidal habitats (Table 2). The exception being the percentage of basal species, which is only 1 %, the lowest value ever reported for a complex food web network, to the best of our knowledge. This is due to the uneven resolution of the food web, with high agglomeration of species at the basal level, and high definition of species at the consumer level. This is common to all highly defined complex food web network studies, and values as low as 2 % have been reported for a Caribbean coral reef, by Opitz (1996), and 3 % for the Northeast US Shelf ecosystem, by Link (2002). It is a consequence of a generalized gap in literature on the specific consumers of macroalgal species, given that the diet descriptions available typically only indicate if the consumer feeds on green, red or brown algae (Nielsen et al., 2018). Often macroalgae can only be identified to species level by observing anatomical structures that are easily destroyed in the digestive process. This issue calls for the use of methods that use DNA analysis to investigate the full array of dietary items of the consumer, such as metabarcoding applied to stomach content analysis (Joly et al., 2014; Cordone et al., 2022). Another alternative is to directly observe the feeding behaviour of species in the wild, to investigate which basal species are consumed and which are avoided. Avoidance of some macroalgal species is to be expected given that they often have chemical defences to deter consumers (Stachowicz and Hay 1999). Very low percentages of basal species are, thus, to be expected in all highly defined food webs assembled for highly speciose systems, until advances occur that allow the match at the species level of macroalgae and seaweeds to their consumers.

While the value of 57.3 links per species reported here is the highest ever observed in an open marine ecosystem, higher values have been reported for coastal lagoons of the Portuguese coast (Vinagre and Gaston 2024), analysed using similar methods. This is due to this web being more highly defined than most of the previous webs, since L/S scales positively with the number of species, as shown by Martinez (1993, 1994) and Dunne et al. (2004).

Purely structural topological food web networks like the one presented here, are useful in simultaneously revealing universal patterns of network organization and also capturing which species assume potentially critical roles (Solé and Montoya; 2001; Montoya et al., 2006). Highly connected species have been identified as critical nodes in the network, since impacts on them can lead to fragmentation of the web and secondary extinctions, when a species is removed because it lost all of its prey species (Solé and Montoya, 2001; Dunne et al., 2002; 2004). If additionally, they present short average path lengths, then such impacts should rapidly reach many other species throughout the network (Montoya et al., 2006; Gaichas and Francis, 2008). The research field of functional food webs, that deals with interaction strength, has also clearly shown the pivotal role of top predators in determining dominance in food webs and how disturbances at the top of the web can easily cascade to bottom levels (Paine, 1974; Carpenter et al., 1985; Estes et al., 1998). This is very useful for ecosystem-based management, since it allows the monitorization efforts to focus on the few species supporting critical network connections (Gaichas and Francis, 2008), instead of trying to study the many thousands of species that make up the food web.

Humans are the top predators in this web. The inclusion of humans in complex food web networks is relatively rare (e.g. Dunne et al., 2016; Vinagre et al., 2019), even though they have an important role as predators in marine ecosystems all over the world. In the present study human predation is established through the fishing of a great variety of fish, crustaceans and cephalopods, as well as the harvesting of bivalves (Supplementary material 2, 3).

Both Dunne et al. (2016), studying the food web of the Sanak Islands of Alaska including pre-modern hunter gatherers, and Vinagre et al. (2019), studying the food web of the Tagus estuary (just 30 km north of the present study area), with modern day fishers, concluded that humans were not only the top TL species but also supergeneralist species. In the present study, humans have 168 prey species (Fig. 2), while in the Sanak Islands and in the Tagus estuary only 70 and 40 prey species were reported for humans, respectively (Dunne et al., 2016; Vinagre et al., 2019). While the present study confirms humans as top predators and highly generalist consumers, they only ranked as the 66th most generalist species. This happens because the present dataset has a high resolution for species which humans do not consume (but other consumers do), unlike the previous studies, which have some resolution bias towards commercial species.

Some high trophic level species were unexpected, showing that several trophic levels can be reached even by small species, although the trophic ecology of small animals tends to be less studied. Among such small animals with high TL was the nudibranch, *Piseinotecus sphaeriferus*. This small animal that rarely exceeds 6 mm in length, has no predators in this food web. It feeds on two species of hydrozoans, which in turn feed on a variety of small invertebrates, like copepods, isopods, amphipods, leptostracans, cumaceans, mysids, tanaidaceans and ostracods (Supplementary material 2, 3), which are mostly primary consumers, feeding on phytoplankton, macroalgae, seaweeds, and/or detritus. Because the basal level is level 1, the small invertebrates are level 2, and the hydrozoans are level 3, this nudibranch is placed near a trophic level of 4 in the web. It also consumes detritus, much like most of the consumers in this food chain, which slightly lowers its trophic level (Supplementary material 2, 3).

The amphipod *Leucothoe incisa* is also among the top 10 species in TL (Table 3). This is a 7 mm carnivorous amphipod, which feeds on detritus, copepods, ostracods and polychaetes (supplementary material 2, 3). Because its diet of polychaetes is not defined to the species level, in the present analysis, its diet was generalized to all species of polychaetes registered in the study area, which in turn feed on a great variety of species of amphipods, cumaceans, other polychaetes, isopods, bivalves, gastropods and echinoderms (supplementary material 2, 3) that may feed directly on the basal level (level 1) or on primary consumers (level 2). Once the polychaete diet of this species is resolved to the species level, it is expectable that it will not feed on all polychaetes, limiting the amount of food chains it feeds on and the amount of loops encompassed in these chains and, thus, lowering its TL. If we compare this amphipod species to other top TL large predators, like the bottlenose dolphin *Tursiops truncatus*, we find that such species have a lower TL. This happens because megafauna species, such as *T. truncatus*, have very well-defined diets, to the species level, feeding mostly on commercial fish and cephalopods, which in turn have very well-defined diets themselves (supplementary material 2, 3). This results in an estimation of TL based on a lower number of much less generalized of food chains, and to a more accurate final value.

Not surprisingly, the other species among the top 10 TL included large sea birds, dolphins and sharks. The common dolphin and the bottlenose dolphin were not just top species but also species with >90 prey species (Fig. 2), thus assuming important roles as supergeneralist top predators. Other important supergeneralist top predators were the eagle ray, *Myliobatis aquila* and the seabream, *Diplodus sargus*, with 507 and 500 prey species, respectively (Fig. 2). The octopus, the top species in landings per unit of effort, in this fishery (Batista et al. 2015), albeit not among the top 10 TL, is also a supergeneralist predator with 325 prey species in this food web.

Two swimming crabs assume important topological roles, *Polybius henslowii* and *Polybius navigator*, as they are both among the top 10 species in connectivity (Table 4) and shortest path length (between node pairs) (Table 7). This places them as important mid TL network nodes, as they occupy the 177th and 136th TL position, respectively. This, along with the seasonal summer population explosions of *P. henslowii* that produce pelagic swarms (González-Gurriarán et al., 1993), is indicative that this species is a particularly important network node for energy flow from the bottom to the top of the web. Diet studies show that *P. henslowii* can be particularly important for seagulls (Munila 1997), demersal fish (Olaso and Rodriguez-Marin 1995) and cephalopods (Castro and Guerra, 1990; Seixas et al., 2020).

The most relevant species from a trophic network point of view is the cuttlefish, *S. officinalis*, a cephalopod of high commercial interest, among the top three species in landings per unit of effort (kg day$^{-1}$ vessel$^{-1}$) (Batista et al., 2015) and a central species in the local gastronomy. The cuttlefish has the highest of all number of prey species (560 species) of all species in the web (Fig. 2) and is among the top 10 most highly connected species (with more direct links to other species) (Table 4). Additionally, the cuttlefish is among the species with lowest mean shortest path length (Table 7), that is the lowest number of chained links connecting it to any other species, which indicates that a disturbance affecting this species is likely to quickly spread throughout the network.

The most likely disturbances for the population of cuttlefish living in this MPA are overfishing, since the species is one of the main targets of local fisheries (Batista et al. 2015), and pollution from the nearby Sado estuary (Costa et al., 2012; Rodrigo et al., 2013). Abecasis et al. (2013), using acoustic telemetry, found that the Arrábida MPA is insufficient to protect cuttlefish. This is because cuttlefish are highly mobile and display low site fidelity, thus travelling well beyond the protected areas of the MPA (Abecasis et al., 2013). In fact, it is thought that cuttlefish from the Arrábida MPA migrate seasonally to the nearby Sado estuary (Batista et al., 2009; Neves et al., 2009), which is rich in seagrasses, a typical cuttlefish habitat. In the Sado estuary, cuttlefish are not only the main target of the local fisheries but also an important prey for the local population of bottlenose dolphins (Santos et al., 2007). However, there they may also be exposed to complex mixtures of pollutants from industrial (shipyards, paper mills, a thermoelectrical plant and chemical industries) (e.g. Caeiro et al., 2005, 2009; Costa et al., 2012) and agricultural sources (mostly rice fields) (Costa et al., 2009; 2011). In fact, Rodrigo et al. (2013) suggested that cuttlefish would be a good choice for a novel bioindicator for risk assessment in impacted estuaries, due to the clear response of oxidative stress biomarkers to pollutants observed in individuals from the Sado estuary. Given the important role of cuttlefish in the food web network of the Arrábida MPA revealed in the present study, as a supergeneralist upper-middle level predator (44th in TL), highly connected to many other species, through short path length, cuttlefish would naturally be indicated as a central species for the focus of management efforts, given that disturbances to such a pivotal node in the network can easily reach all other species. The fact that this species is also one of the main target species of local fisheries and that it extends its territory to areas outside the protection limits of the MPA, where it is the main target of another fishery and where it is exposed to pollution, make this a particular case for ecosystem-based management where a clear demand exists for continuous and close monitorization of the population health of cuttlefish not only in the Arrábida MPA but also in the adjacent estuary of the Sado river.

Landings per unit effort (LPUE), an index of relative abundance, are available for cuttlefish from the official auctions (www.DocaPesca.pt), where commercial fishers are obliged to land their catches and where daily landing statistics are recorded by vessel. Biological sampling of landings is also carried out by the national fisheries institute (IPMA), providing additional information, such as size distributions (Azevedo et al., 2021). However, given that most cuttlefish only live one year, environmentally driven recruitment variability is the main factor affecting the abundance and availability of cuttlefish. This means that output management measures such as total allowable catch, that require estimates of stock biomass, cannot be implemented.

Nevertheless, monitoring the cuttlefish population in the study area is important to understand its population dynamics and general health. We recommend a monitoring program directed at the Arrábida-Sado cuttlefish based on landings per unit effort (LPUE). This could be done quite effectively by obtaining the official daily landings data per vessel for Sesimbra and Setúbal, the two ports where cuttlefish caught in Arrábida and the Sado estuary, are landed, and assuming that the unit of effort is "trip". Onboard monitoring of the vessels involved could help refine the estimates of LPUE and ensure that undersized cuttlefish are not caught. Tracking the fishing vessels using GPS based systems would provide very detailed information on fishing effort, while implementing onboard cameras for remote inspection would lower the costs of the onboard monitoring operations.

Expanding the existing telemetry studies for cuttlefish that use the Arrábida MPA (Abecasis et al., 2013) and the Sado estuary would be very important to improve the understanding of movement ecology and habitat connectivity for this species, in this area. Conservation of cuttlefish in the region is highly dependent on the conservation of their primary habitat, which are the seagrass meadows. These have been subject of a reintroduction program (BIOMARES project). However, seagrasses still occupy a very small proportion of their past habitat area. Expanding and reinforcing this program would be very important for cuttlefish and all other seagrass-associated species.

Monitoring of the accumulation and response to contaminants in cuttlefish would be very important, as transition ecosystems are paramount breeding and nursery grounds for these ecologically and economically important animals that have been found to be sensitive to heterogenous and mostly diffuse pollution in the Sado basin (Rodrigo et al., 2013; Costa et al., 2014). We recommend yearly sampling of adults, juveniles and eggs, in the Arrábida MPA and in the Sado estuary, for the analysis of legacy toxicants, namely metals and persistent organic pollutants, plus chemicals of emerging concern such as endocrine disruptors. To this should be added biomarkers of effects and exposure in gills and digestive glands, which would provide a general picture of the animals' condition and ability to respond to exposure. During the BIOMARES project (2007–2010) (Cunha et al., 2014) the Arrábida MPA fishermen always blamed pollution from the Sado river for the decline in catch and loss of seagrass habitats inside the MPA, instead of overfishing, which is accordant with subsequent work integrating environmental characterisation, biomonitoring and epidemiology (Caeiro et al., 2017). Cuttlefish ecotoxicology and its deployment as sentinel for biomonitoring is thus an important component of environmental risk assessment for this vast and critically important estuarine basin and adjacent MPA.

Notwithstanding, the most critical measure to be implemented is the systematic monitoring of illegal activities within the MPA, coupled with the rigorous enforcement of fishing regulations across the area, to ensure the effective protection of habitats and all species within it.Lastly, we recommend that the present study is expanded to incorporate fluxes of biomass and energy in the food web network, addressing the major limitation of purely topological approaches like the present one, which is providing practical ecological dynamics meaning and analysis of likelihood of changes in biomass given perturbations. For such to be possible, more studies are needed to inform on the site fidelity to the MPA, of all species, their biomass per area, metabolic rates, consumption rates, etc. Such information can be coupled to the complex food web assembled in the present work.

## CRediT authorship contribution statement

**Catarina Vinagre:** Writing – review & editing, Writing – original draft, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Luís Almeida:** Writing – review & editing, Investigation, Formal analysis, Data curation. **Pilar Ronquillo:** Writing – review & editing, Investigation, Formal analysis. **Vanessa Mendonça:** Writing – review & editing, Investigation, Formal analysis. **Duarte Frade:** Writing – review & editing, Investigation, Data curation. **Emanuel J. Gonçalves:** Writing – review & editing, Supervision, Resources, Investigation. **Karim Erzini:** Writing – review & editing, Supervision, Resources, Investigation. **Ester A. Serrão:** Writing – review & editing, Supervision, Resources, Project administration, Investigation, Funding acquisition.

## Declaration of competing interest

The authors declare no competing or financial interests.

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## Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.ecocom.2025.101134.

## Data availability

The data is available in the supplementary material.

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